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1. SITE AND VEGETATION

Measurements were made during May to October, 1987 and June to August, 1989 over a tallgrass prairie near Manhattan, Kansas (39° 03' N, 96° 32' W, 445 m above m.s.l.). Soil at the experimental site is predominantly Dwight silty clay loam (Typic Natrustolls). The prairie was burned on 16 April, 1987 and on 28 April, 1989 to improve the mix of grasses and forbs. The experimental area was not grazed during 1986-1989.

Percent species composition at the study site was estimated by employing a modified step-point method (Owensby, 1973). The vegetation is dominated by three warm season C_4 grasses: big bluestem (*Andropogon gerardii*), indiangrass (*Sorghastrum nutans*) and switchgrass (*Panicum virgatum*). Numerous other grasses, sedges, forbs and woody plants constitute the remainder of the plant community.

2. PLANT AND SOIL MEASUREMENTS

Plant growth was monitored on a regular basis by measuring plant height, dry matter and leaf area. Leaf area index (LAI) was measured with a portable area meter (LI-COR, Inc., Lincoln, NE, Model LI-3000).

The surface soil water content (0-0.1 m) was monitored gravimetrically and subsurface water content (0.1-1.4 m) was measured with a neutron probe (Campbell Pacific Nuclear Corp., Pacheco, CA, Model 503) on a weekly basis. The neutron probe was calibrated at the field site prior to the experiment.

3. MICROMETEOROLOGICAL MEASUREMENTS

Eddy Correlation Measurements. The eddy correlation technique (for example, Kaimal, 1975; Kanemasu *et al.*, 1979; Verma, 1990) was used to measure the fluxes of momentum (τ), sensible heat (H), latent heat (λE), and carbon dioxide (F_c). The instrumentation included a three-dimensional sonic anemometer (Kaijo Denki Company, Tokyo, Japan, Model DAT-310), one-dimensional sonic anemometers (Kaijo Denki Company, Model DAT-110; Campbell Scientific, Logan, Utah, Model

CA27), fine-wire (0.025 mm) thermocouples (Campbell Scientific, Model 127), a Lyman-alpha hygrometer (A.I.R., Inc., Boulder, Colorado, Model LA-1) with a 5-mm path length, a Krypton hygrometer (Campbell Scientific, Model KH20) with a 10-mm path length, and a rapid response CO_2 sensor with a 0.2-m path length (Bingham *et al.*, 1978; Anderson *et al.*, 1984). These sensors were mounted on a horizontal boom 2.25 m above the ground. The data were low-pass-filtered using eight-pole Butterworth active filters with 12.5-Hz cutoff frequency. The signals were sampled at 20 Hz. Sampling, recording, and near-real-time processing of the data were done with an IBM PC-AT microcomputer [details are available in previous reports, for example, Verma *et al.* (1986, 1989)]. Fluxes were obtained from covariances computed over 30-min. averaging periods. Covariance values were corrected for the effects of spatial separation of sensors following the method of Moore (1986). The latent heat and CO_2 fluxes were corrected for the variation in air density due to simultaneous transfers of sensible heat and water vapor following the method of Webb *et al.* (1980).

Bowen Ratio-Energy Balance and Other Supporting Measurements. Fluxes of latent and sensible heat were also measured employing the Bowen ratio-energy balance technique. Precisely calibrated ceramic wick psychrometers were used. The temperature sensors were made of Ni-Fe resistance thermometers (Minco Products, Minneapolis, MN, Ni-Fe RTD). The wet bulb element is a porous ceramic tube operating under a water supply with a positive head. The supply was adequate for one week of operation without refilling. Pairs of psychrometers were mounted on two adjacent masts. The vertical separation between the psychrometers on each mast was either 0.9 or 1.0 m. Each pair of psychrometers was interchanged every five minutes to minimize the effect of instrument bias. Before, during and after the experiment, the resistance temperature sensors were calibrated against a platinum resistance thermometer in a temperature calibration system consisting of a refrigerated bath and circulator with precise temperature regulation (HAAKE, Inc., Saddle Brook, NJ, Model A-80).

Net radiation (Rn) and incoming photosynthetically active radiation (K_{PAR}) were measured with net radiometers (Radiation Energy Balance System, Beaverton, Oregon) and quantum sensors (LI-COR, Inc., Lincoln, Nebraska) located 2.0 m above the ground. Surface soil heat flux was estimated by employing a combination method (Kimball *et al.*, 1976) in which a heat flow transducer is placed at a certain depth in the soil, and the averaged soil temperature above it is used to estimate the amount of heat stored in that layer. Seven heat flow transducers (Micromet System, Beaverton, OR, Model HFT-1) were installed at a depth of 50 mm. The average soil temperature from the surface to 50 mm was measured with 18 platinum resistance thermometers (0.2 m long) buried at an angle of about 15 degrees. The platinum resistance thermometers were calibrated in the laboratory against a standard platinum resistance thermometer in a temperature calibration system. Heat flow transducers were calibrated at the factory. Since the thermal conductivity of the calibration medium was not the same as that of the heat flow transducer, measured heat flux was corrected for this difference by employing a method described by Philip (1961). Correction due to the difference in thermal conductivities of the heat transducer and the soil was also made. Data on volumetric water content in the surface soil (0 to 10 mm), measured each day from selected locations at the site, and precipitation were used to estimate the heat capacity of the soil.

Mean wind speed was measured with three-cup anemometers (Cayuga Development, Ithaca, NY, Model WP-1) at 1.00, 1.25, 1.50, 1.75, 2.00, 2.25 and 2.75 m heights. Cassela three-cup anemometers [Science Assoc., Princeton, NY, Model 422(2)] were also used. Anemometers were calibrated in the field against a standard anemometer before, during and after the experiment. Wind direction was measured with a wind vane.

4. SUMMARY OF RESULTS

Detailed discussion of analyses and results are provided in the journal articles cited in Sec. 5. A brief summary of results is given below.

A. Soil Moisture and Plant Growth

Precipitation was generally ample from May to September in 1987, except during 3 weeks in late July to early August. Extractable soil water (W_E) of the primary root zone (0-1.4 m) was generally above 50% during May through September except during the dry period (late July to early

August). During the dry period, W_B was as low as 25% and moisture stress conditions prevailed. The green LAI reached its maximum of about 3.2 toward the end of June in 1987, during the peak growth stage, and gradually decreased with senescence of the prairie vegetation.

In 1989, a prolonged spring drought caused a delay in plant growth. With frequent rainfall in June, the prairie vegetation began to grow rapidly. However, another dry spell occurred in early July, and the prairie was under moisture stress conditions for 2 weeks. Following ample rainfall in mid-July to August, the vegetation recovered from the moisture stress and the green LAI reached its maximum of 2 in early August.

B. Momentum Flux and Canopy Aerodynamic Characteristics

The drag coefficient ($C_d = u_*^2/\bar{u}^2$, where u_* is the friction velocity and $\bar{u}$ is the mean wind speed at 2.25 m above the ground) of the prairie vegetation ranged from 0.0087 to 0.0099. Over a mixed-grass prairie (canopy height, $z_c \approx 0.1$ to 0.3 m) in Saskatchewan, Canada, Ripley and Redmann (1976) reported values of C_d ranging from 0.0093 at $\bar{u} = 2$ m s^{-1} to 0.0046 at $\bar{u} = 15$ m s^{-1} ($\bar{u}$ was measured at a height of 2 m).

The average d/z_c and z_o/z_c (where d is the zero plane displacement, z_o is the roughness parameter and z_c is the canopy height) were estimated to be about 0.71 and 0.028, respectively. The literature values of d/z_c and z_o/z_c from agricultural crops (for example, beans, cotton, potatoes, wheat) and a mixed-grass prairie range respectively from 0.56 to 0.79 and 0.041 to 0.160 (Thom, 1971; Munro and Oke, 1973; Legg and Long, 1975; Ripley and Redman, 1976; Bache and Unsworth, 1977; Legg *et al.*, 1981). Information was developed on the aerodynamic conductance (g_a) in terms of mean wind speed ($\bar{u}$ measured at a reference height) for different periods in the growing season. As expected, there was a near-linear relationship between g_a and $\bar{u}$.

C. Evapotranspiration, Components of Energy Balance and Canopy Conductance

During the early and peak growth stages, with favorable soil moisture, the daily evapotranspiration (ET) rates ranged from 3.9 to 6.6 mm day^{-1}. On a few days (for example, July 10 and July 11, 1987), when soil moisture was plentiful, the evaporative demand was high primarily due to strong winds, and the ET rates exceeded the available energy (Q_A = Rn-G) by 5%-10%. The ET rate during the dry period was between 2.9 and 3.8 mm day^{-1}. During mid-August to early September, ET recovered to an average rate of 5.1 mm day^{-1}. The ET rates decreased to 0.7-0.9 mm day^{-1} during plant senescence in October.

The value of the Priestley-Taylor coefficient (α), calculated as the ratio of the measured ET to the equilibrium ET, averaged around 1.26 when the canopy stomatal resistance (r_c) was less than 100 s m^{-1}. When r_c increased above 100 s m^{-1}, α decreased rapidly, as was also observed in the simulation study of McNaughton and Spriggs (1989).

During the period of most vigorous plant growth (for example, June-July, 1987) with favorable soil moisture, midday λE averaged about 0.69 Rn and the Bowen ratio (β) was about 0.25. Daily patterns of λE and H followed that of Rn. The canopy surface conductance (g_c, computed from the Penman-Monteith equation) followed the diurnal pattern of Rn, as did the stomatal conductance of individual leaves (measured with a steady-state porometer). The midday averages of the aerodynamic and canopy surface conductances were about 30 and 15 mm s^{-1}, respectively.

The dry spell encountered in late July in 1987 caused a substantial decrease in g_c (midday value $\approx$ 3.0 mm s^{-1}). Like that of the stomatal conductance of the individual leaves, the diurnal pattern of g_c during this period did not respond to Rn. Midday λE was reduced to 0.40 Rn and β averaged about 1.03.

The magnitude of λE increased again after rainfall in mid-August in 1987. It rapidly decreased in September and October with plant senescence. Canopy surface conductance showed a seasonal pattern generally similar to that of λE. With rainfall (in mid-August) following the dry spell, g_c recovered to only 50 to 60 percent of the early season magnitude whereas λE recovered almost fully.

D. Modeling Canopy Stomatal Conductance

Field measurements of stomatal conductance were used to develop a leaf stomatal conductance model for major C_4 grass species in this temperate grassland ecosystem. Employing data on incoming photosynthetically active radiation, vapor pressure deficit, green leaf area index and extractable soil water, the stomatal conductance model was scaled up from a leaf to a canopy level. Values of canopy stomatal conductance, estimated employing this approach, were compared with those of canopy surface conductance computed from measured fluxes using the Penman-Monteith equation. Diurnal patterns and magnitudes of the two estimates were in good agreement under well-watered conditions. Under moisture stress conditions, the agreement was poor. We substituted the daily extractable soil water input with the hourly measurements of leaf water potential. Although the model with the leaf water potential input did not produce any significant improvement in predicting the magnitude of canopy stomatal conductance under moisture stress conditions, it did simulate the diurnal patterns (*e.g.*, morning peak) adequately.

The evapotranspiration rates computed from the modeled canopy stomatal conductance were generally in good agreement with those measured with the micrometeorological eddy correlation technique, except in moisture stress conditions. The failure of the model under these conditions could be attributed partly to the errors associated with the measurement of effective green leaf area when leaves were rolled and folded due to severe water stress.

E. Canopy Photosynthesis, Photosynthetic Efficiency and Water Use Efficiency

The atmospheric CO_2 flux data (eddy correlation) were used, in conjunction with estimated soil CO_2 flux, to evaluate canopy photosynthesis (P_c). The dependence of P_c on photosynthetically active radiation (K_{PAR}), vapor pressure deficit, and soil moisture was examined. Under nonlimiting soil moisture conditions, P_c was primarily controlled by K_{PAR} through a rectangular hyperbolic relationship. Our data did not indicate light saturation of the canopy up to K_{PAR} levels of 2100 μEi m^{-2} s^{-1}. Midday values of P_c reached a seasonal peak of 1.4-1.5 mg m^{-2} (ground area) s^{-1} during late June and early July in 1987. During the dry period (late July to early August), midday P_c declined to a minimum of almost zero. Examination of data on P_c, $\lambda E/Rn$ (the proportion of net radiation consumed in latent heat flux), extractable soil water, and the pre-dawn leaf water potential indicated a remarkable similarity in overall patterns throughout the season.

The photosynthetic efficiency of the prairie vegetation can be expressed in terms of $\mu P_c/Rn$. The term μ is the energy equivalent of photosynthesis and was assumed to be equal to 10.5 kJ g^{-1} (Denmead, 1969). The midday value of $\mu P_c/Rn$ was about 2% in the early and peak growth stages (except during the dry period) and 1%-1.5% in the early senescence stage. Uchijima (1976) found the photosynthetic efficiency (expressed in terms of solar irradiance) of corn to range from 3.1% to 7.4%. Other results reported in the literature include midday $\mu F_c/Rn$ values of 2.1% for wheat (Denmead, 1969), and 1.5%-3.5% for coniferous and deciduous forests (Denmead, 1969; Jarvis *et al.*, 1976; Verma *et al.*, 1986) (note these values are based on the atmospheric CO_2 flux, F_c).

In agricultural studies, water use efficiency (WUE) has been defined as the ratio of canopy photosynthesis (P_c) and canopy transpiration (TR). As a first approximation, we estimated soil evaporation by partitioning the available energy at the soil surface, Q_{AS} (= Rn_s - G), using the Priestley-Taylor (1972) potential evaporation equation with the coefficient, α = 1.26 (net radiation at the soil surface, Rn_s, was estimated using Beer's Law with the measured LAI and the above-canopy Rn, assuming an extinction coefficient of 0.5). These calculations were performed on four selected days (July 2, 6, 10, and 11, 1987), characterized by nonlimiting soil moisture conditions, during the peak growth stage.

Canopy transpiration was calculated using the measured latent heat flux and estimated soil evaporation data. These values of TR were used in conjunction with P_c to compute WUE of the prairie vegetation. Midday values of WUE were fairly stable near 8-12 x 10^{-3} g CO_2/g H_2O (the uncertainty in estimation of soil evaporation can affect these WUE values by 10-20%). Zur and Jones (1984) reported midday WUE values of 5 x 10^{-3} g CO_2/g H_2O for a soybean crop. Data reported by Sinclair *et al.* (1975) and Reicosky (1990) would indicate a daytime value of about 16 x 10^{-3} g CO_2/g H_2O for well-watered corn.

F. Modeling Canopy Photosynthesis

A biochemical model of leaf photosynthesis, in conjunction with a stomatal conductance model, was applied to C_4 tallgrass species (*Andropogon gerardii, Sorghastrum nutans, Panicum virgatum*) The modeled photosynthetic rates of individual leaves were scaled up to the canopy level using a simple canopy radiative transfer model. Comparisons with field measurements, using the micrometeorological eddy correlation technique, showed that the model simulated the magnitudes and the diurnal variations of canopy photosynthesis adequately under well-watered conditions. Although the model overestimated measured canopy photosynthesis by 4-7 μmol m^{-2} s^{-1} under moisture stress conditions, it did seem to simulate the diurnal patterns (*e.g.*, morning peak) realistically. Using similar scaling-up procedures, values of canopy stomatal conductance were also computed from the model. The modeled canopy stomatal conductance agreed with measured values reasonably well (within 0.2 mol m^{-2} s^{-1} under well-watered conditions and within 0.05 mol m^{-2} s^{-1} under moisture stress conditions).

G. Carbon Dioxide Budget in a Temperate Grassland Ecosystem

Eddy correlation measurements of CO_2 flux made during May-October in 1987 and June-August in 1989 were employed, in conjunction with simulated data, to examine the net exchange of CO_2 in a temperate grassland ecosystem. Simulated estimates of CO_2 uptake were used when flux measurements were not available. These estimates were based on daily intercepted photosynthetically active radiation, air temperature and extractable soil water. Soil CO_2 flux and dark respiration of the aerial part of plants were estimated using the relationships developed by Norman *et al.* (1992) and Polley *et al.* (1992) at the study site.

Our results indicate that the CO_2 exchange between this ecosystem and the atmosphere is highly variable. The net ecosystem CO_2 exchange reached its peak value (12-18 g m^{-2} day^{-1}) during the period when the leaf area index was maximum. Drought, a frequent occurrence in this region, can change this ecosystem from a sink to a source of atmospheric CO_2. The degree to which this grassland can become a source of CO_2 appears to depend not only on the severity and duration of the drought, but also on the timing of the drought event in relation to the growth stage of the prairie vegetation. Comparison with data on dry matter indicated that the above-ground biomass accounted for about 45-70% of the net carbon uptake, suggesting the importance of the below-ground biomass in estimating net primary productivity in this ecosystem.

H. Photosynthesis and Stomatal Conductance Related to Reflectance on the Canopy Scale

Using our data, both on the leaf level (*e.g.*, stomatal conductance of the three dominant species) and the canopy level (*e.g.*, water vapor flux), empirical relationships for the environmental stress factors, $f(D)$ and $f(W_E)$, were developed to account for the effect of ambient vapor pressure deficit (D) and extractable soil water (W_E). These factors were then used in conjunction with the measured surface fluxes to compute unstressed canopy conductance (g_c^*) and unstressed canopy photosynthesis (P_c^*).

The derivatives ($\partial g_c^*/\partial PAR$ and $\partial P_c^*/\partial PAR$) of unstressed canopy conductance and unstressed canopy photosynthesis are dependent on the amount and type of green vegetation, and therefore, should be amenable to remote sensing. The analysis of Sellers (1987) indicated that $\partial g_c^*/\partial PAR$ and $\partial P_c^*/\partial PAR$ should be near-linearly related to SR and the first order, preliminary analysis of data collected in this study seems to support this hypothesis. However, before such relationships can be employed in satellite remote sensing applications, more work is needed. Future studies should include: (a) adequate allowance of soil evaporation in calculating canopy conductance, (b) direct measurement of soil respiration, (c) further development and evaluation of environmental stress functions and (d) more frequent measurements of canopy reflectance under similar illumination conditions.

5. SCIENTIFIC PUBLICATIONS AND PRESENTATIONS STEMMING FROM GRANT NAG5-890

The following scientific publications and presentations stem from our work on Grant No. NAG5-890.

Journal Articles

Hall, F. G., P. J. Sellers, I. McPherson, R. D. Kelly, S. B. Verma, R. Markham, B. L. Blad, J. Wang and D. E. Strebel. 1989. FIFE: Analysis and Results—A Review. Advances in Space Research. Cospar Publication 9:275-293.

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